

On the Quantification of Suckling Intensity in Primates

RODNEY L. JOHNSON,^{1*} IQBAL MALIK,² AND CAROL M. BERMAN³

¹Charles River–Key Lois, Summerland Key, Florida 33042

²Vata Varan, New Delhi 110049, India

³Department of Anthropology, State University of New York, Buffalo, New York 14261

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ABSTRACT The inhibitory effect that suckling has on the reproductive function of primate mothers varies as a function of the intensity with which they are suckled. Here we present an easily computed index of one parameter of suckling intensity, namely the temporal patterning of suckling bouts. High intensity suckling is characterized by frequent nursing bouts demarcated by short interbout intervals. Therefore, our suckling index is based on the brevity of observed interbout intervals, more specifically the proportion of such intervals that fail to exceed a criterion length. The index is an appropriate means of making interspecific comparisons of the development of infant suckling and is well suited for application to field data that include interbout intervals that were not observed in their entirety. To demonstrate its utility, we apply the index to field data collected on the suckling behavior of free-ranging rhesus monkey (*Macaca mulatta*) infants in India. In this context, we demonstrate that, in rhesus, between-infant differences in suckling intensity manifest themselves early in the postpartum period and contribute to between-female differences in the timing of first mating postpartum. *Am J Phys Anthropol* 105:33–42, 1998. © 1998 Wiley-Liss, Inc.

Suckling intensity varies not only as a function of the vigor with which infants suck but also the temporal patterning (i.e., structure [Vitzthum, 1994]) of nursing bouts (Jones, 1988). High intensity suckling is characterized by frequent nursing bouts demarcated by short interbout intervals and is the kind of suckling that inhibits the postpartum resumption of normal reproductive function in primate females, human and nonhuman. The mechanical stimulation of the nipple that occurs at the onset of a suckling bout produces afferent nerve impulses that are transmitted to the hypothalamus. The mechanism by which the patterning of suckling bouts (and therefore the patterning of sensory input to the hypothalamus) forestalls the return of ovulatory cycling remains obscure, but disruption of the hypothalamic release of gonadotropin releasing

hormone is currently considered to be the probable final pathway (McNeilly et al., 1994; Vitzthum, 1994; Zinaman et al., 1995).

The studies of nursing nonhuman primate mothers conducted to date (e.g., Nicolson, 1982; Lee, 1987; Stewart, 1988) have relied on the number of nursing bouts occurring per unit time (hereafter referred to as the bout rate) to quantify the intensity of suckling. Rhesus monkeys (*Macaca mulatta*) have been the subjects of several of these studies (e.g., Wilson et al., 1988; Gomendio, 1989; Berman et al., 1993), and for females of this

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*Correspondence to: Rodney Johnson, PO Box 420375, Summerland Key, FL 33042-0375. E-mail: rodjohn@juno.com

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species the bout rate has been shown to be a reproductively relevant measure of nursing behavior 6–8 months postpartum. Here we describe an alternative measure of suckling intensity (hereafter referred to as the suckling index) that is as easily computed as the bout rate but is based on the intervals between nursing bouts. By applying the suckling index to data collected on free-ranging rhesus mothers in India, we illustrate the important advantage that the index has relative to the bout rate, namely that it can be applied usefully to the suckling behavior of all neonates, even the very youngest.

The present paper is not the first to examine interbout intervals. Some studies of the contraceptive effect of nursing in women have used the mean and/or maximum length of interbout intervals to quantify the patterning of nursing bouts (e.g., Konner and Worthman, 1980; Stern et al., 1986; Vitzthum, 1989; Campbell and Gray, 1993). In general, the research attention paid to interbout intervals has paralleled that in prolactin, the pituitary hormone once thought to be the principal agent for lactational anovulation. Serum prolactin levels increase rapidly following the onset of a suckling bout and remain elevated for about 2 h after suckling has been terminated (Howie et al., 1979). As a consequence, it was initially suggested that nursing mothers would remain acyclic as long as their serum prolactin remained tonically high, as would occur if the intervals between nursing bouts stayed brief (Konner and Worthman, 1980). Prolactin is no longer considered to be principally responsible for lactational anovulation either in women (McNeilly et al., 1994; Vitzthum, 1994) or female rhesus monkeys (Gordon et al., 1995). Instead, it is considered (at least by some investigators [e.g., Wood, 1994; Stallings et al., 1996]) to be an indicator of the “strength” (Lunn, 1994) of the sensory signal reaching the hypothalamus of a nursing mother. Nevertheless, breastfeeding women are indeed significantly more likely to remain acyclic if their serum prolactin concentration remains elevated throughout their interbout intervals (Stallings et al., 1996), an unlikely occurrence if their intervals are especially protracted.

Howie and McNeilly (1982) concluded that women wishing to exploit the contraceptive effect of breastfeeding should be advised to “avoid long intervals” (p. 556) between nursing bouts. The index of suckling described in the present paper provides investigators with a potential means for exploring the question of what constitutes a long interbout interval. Here we provide a provisional answer for female rhesus monkeys and demonstrate that, in rhesus, between-infant differences in the incidence of long interbout intervals contribute to between-female differences in the timing of first mating postpartum. Since the timing of mating onset in rhesus females is indicative of the animals’ resumption of ovulatory cycling (Gordon, 1981; Wallen, 1990), we also address the possible applicability of the suckling index to studies of the postpartum return of ovulation in nursing women.

METHODS

Subjects and collection data

The data presented here were collected as part of a larger study of mother-infant relations among the seasonally breeding rhesus monkeys resident at Tughlaqabad, a fourteenth-century fort located southeast of New Delhi, India (for detailed description of the site see Malik et al., 1985; Johnson et al., 1991). Our adult female subjects belonged to either of two social groups (Johnson et al., 1993) and were individually recognized. During data collection they were encountered daily. Hence, their dates of parturition are known exactly. Each mother’s resumption of sexual activity during the mating season was recorded when she was first seen to copulate or was first sighted with a white, vaginal plug of coagulated ejaculate. Since rhesus females often mate surreptitiously (McMillan, 1989), the date of first mating for some of our subjects was probably not recorded with the same accuracy as was the date of parturition. Nevertheless, we feel confident that the difference between the actual and recorded date of mating onset was in no case greater than 3 days.

Twenty rhesus mothers contributed data to the present paper. They constitute that subset of all Tughlaqabad mothers we observed that unequivocally resumed mating

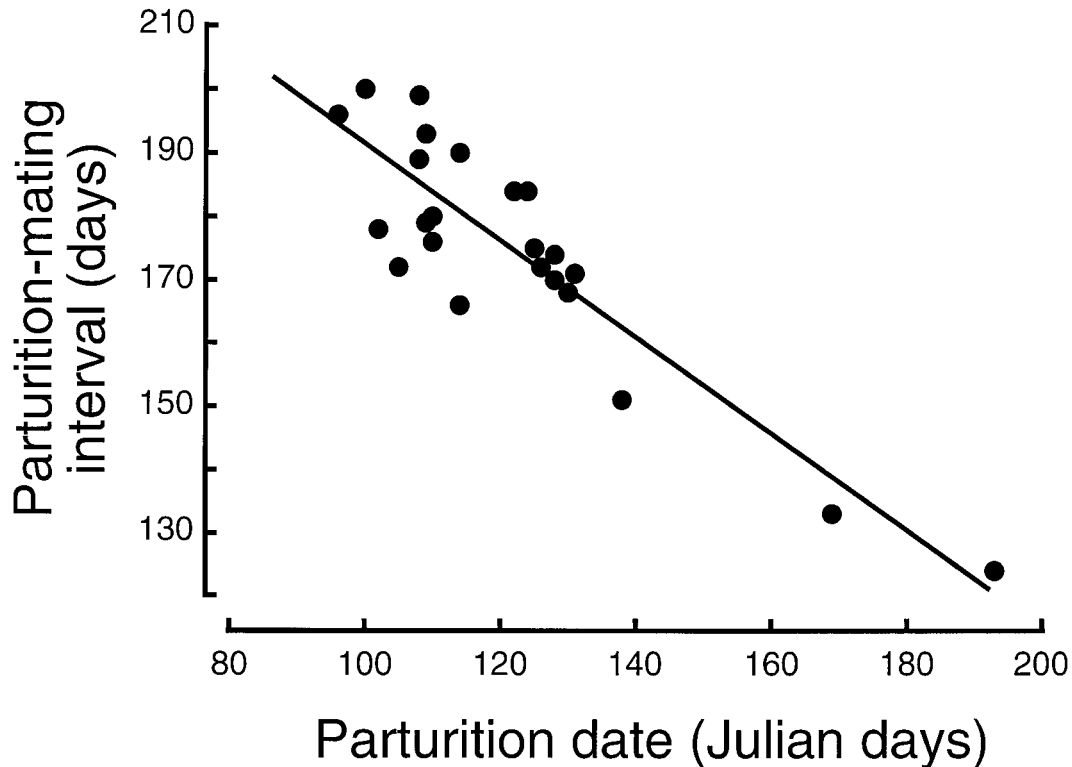


Fig. 1. Regression of parturition-mating interval (PMI) length on parturition date (in Julian days). This plot is based on the parturitions and mating onsets of all of the adult females in our study groups that gave birth in 1988 and illustrates the means by which expected PMIs were calculated. See text for explanation and regression statistics.

postpartum either 1) earlier or 2) later than expected. The expected rapidity with which our subjects resumed mating was based not on the calendar dates of their respective mating onsets but instead on their parturition-mating intervals (PMIs)—that is, the number of days elapsed between their dates of delivery and dates of first mating. In rhesus, PMI length is inversely related to and primarily determined by the timing of parturition during the birth season (Malik et al., 1992; Johnson et al., 1993). To illustrate, in Figure 1 the observed PMIs of all of the adult females ($n = 23$) in our Tughlaqabad study groups that gave birth in 1988 are regressed on their parturition dates (in Julian days). The fitted regression is negative ($r = -0.89$), highly significant ($P < 0.01$), and accounts for almost 80% of the variance ($r^2 = 0.79$) in the observed parturition-mating intervals. In Figure 1, the

data points located below the fitted regression line and those positioned above it represent, respectively, females whose observed PMIs were shorter or longer than expected on the basis of the animals' parturition dates alone. The unequivocally early and late mothers of the present paper were, again respectively, those whose observed PMIs were at least 5 days shorter or 5 days longer than expected (early: range = 5–15 days early; late: range = 6–14 days late). A 5 day difference between observed and expected PMIs was used to select subjects for the present paper because this value conservatively exceeds the 3 day error (see above) potentially present in some of our subjects' recorded dates of first mating. (The disparity between the females' observed and expected PMIs was obtained by saving the residuals generated by the hierarchical regression analysis summarized in Table III of

TABLE 1. Number of late and early mothers observed and mean number of observation hours per mother (and range) accumulated during each of the first 8 months¹ postpartum

Maternal category	Months postpartum							
	1	2	3	4	5	6	7	8
Late								
Number	9	10	10	10	10	10	9	8
Mean hours	14.8	16.1	16.1	16.5	18.5	19.2	18.7	18.8
Range	11.7–19.5	13.7–20.9	13.8–20.1	12.5–19.2	17.0–20.2	17.8–20.6	16.2–20.7	14.9–20.9
Early								
Number	10	9	8	10	10	10	10	8
Mean hours	15.3	15.6	15.7	16.5	17.3	17.9	18.4	18.9
Range	14.2–17.6	12.5–21.0	10.0–18.0	14.0–18.6	14.5–19.7	12.8–20.4	15.4–20.9	15.7–20.2

¹ Each postpartum month represents a period of 4 weeks.

Johnson et al. (1993). This analysis included PMI data from two other rhesus populations in addition to Tughlaqabad, and the large sample of PMIs allowed for a more accurate calculation of expected PMI lengths for the Tughlaqabad mothers than could be obtained from a regression based on our Indian data alone.)

The late and early mothers of this paper were observed during focal animal (Altmann, 1974) sessions generally conducted three times per fortnight, twice in the morning and once in the afternoon. Data collection on a given female usually commenced 1–5 days after her parturition. However, for a few of our subjects observed in 1987, data collection did not begin until later, as late as the seventh week postpartum in one instance. Further, particularly severe monsoon storms and the intensity of the observation schedule itself sometimes precluded observing all females during all fortnights. The focal observational sessions were approximately 30–40 min long during the weeks immediately following parturition but were progressively lengthened to a maximum of 3.5 h by about the twentieth week postpartum. Data were collected by three observers, and frequent interobserver checks assured close agreement on the scoring of these contacts. The data from eight successive 4 week periods (referred to here as the first 8 months postpartum) were analyzed for the present paper. The number of late and early mothers observed during each month and the range and the mean number of observational hours accumulated per female are provided in Table 1.

During the focal sessions, a continuous record was kept of all instances of infants

orally contacting their mothers' nipples. Observational conditions at Tughlaqabad generally were quite good. Nevertheless, we were not able to observe our subjects from as close a range as would be necessary to enable us to distinguish between nonnutritive and nutritive suckling (i.e., <1 m [see Tanaka, 1992]). We therefore operationally defined a suckling bout as a series of nipple contacts demarcated by periods of noncontact of at least 5 min duration, the length of the shortest interbout interval recognized in this study. Because nipple contacts made by very young rhesus infants often occur in very brief strings, we did allow that interbout intervals longer than 10 min could subsume some nipple contacts but only if such contacts occurred in strings lasting less than 1 min and were both preceded and followed by at least 5 min of noncontact. Our definitions of the suckling bout and interbout interval greatly facilitated the tabulation of our data. They also reflect our expectation that brief interruptions of nursing and even briefer temporally isolated strings of suckling are likely to be of little reproductive relevance to rhesus mothers.

Suckling index

Application of the suckling index requires that a criterion interval length be employed to differentiate between short and long interbout intervals; long intervals are those that exceed the criterion, while short intervals do not. Computation of the index takes the form $f_S / (f_S + f_L)$, where f_S is the frequency of short interbout intervals and f_L is the frequency of long interbout intervals. Thus, the index is the proportion of all intervals realized by a given mother-infant pair at a given

infant age that, by definition, are short. Being a proportional measure, the index ranges from a maximum of 1.0 (when all interbout intervals are short) to a minimum of 0.0 (when all intervals are long).

In order to gain insight into how long a long interbout interval is for rhesus mothers, we employed three alternative criteria for differentiating between such intervals and their short counterparts: 15, 30, and 45 min. In other words, the suckling index was first calculated with long intervals defined as those interruptions of nipple contact that were of 15 min duration or longer; short intervals were those lasting less than 15 min. The index was then recalculated twice more, once with long intervals defined as those at least 30 min long and once again with long intervals defined as those lasting at least 45 min.

All interbout intervals were used in the computation of the suckling index, even censored intervals (i.e., those not observed in their entirety because they were in progress either at the start or close of our observational sessions). As one would expect, the most protracted intervals underwent censoring most often; almost half of all intervals known to have lasted longer than 45 min were censored. Of course, computation of the suckling index was unaffected by the inclusion of intervals truncated after 45 min. However, when computation of the suckling index was based on the 45 min criterion, using intervals truncated before this (but had, in fact, lasted longer than 45 min) necessarily inflated the number of short interbout intervals we recorded and, therefore, the calculated index scores as well. Inasmuch as the data from all mother-infant pairs were subject to this same inflationary effect, the relative differences between dyads were maintained (cf. Vitzthum, 1989), and statistically significant differences found in the suckling index scores of our subjects certainly exist despite (not because of) our use of censored intervals.

We hypothesized that the early mothers at Tughlaqabad resumed sexual activity more rapidly than did the late mothers at least in part because they had been suckled less intensively prior to their mating onsets (Johnson et al., 1993). The data included in

the present paper do not speak to the question of why some mothers nurse their infants more intensively than others; this topic will be addressed in a later paper (but also see Johnson et al., 1993). The analyses included here are designed instead to determine which measure of suckling best differentiates between the nursing behavior of late and early mothers, especially in terms of when (i.e., the postpartum month) between-dyad differences in suckling intensity first manifest themselves. To answer this question, we contrast the suckling index and bout rate scores of late and early mothers by means of one-tailed *t*-tests. Given that the suckling index is a proportional measure, the arcsine transformation was applied to the data for this variable prior to the execution of all such contrasts. However, in this report it is the untransformed data that are depicted graphically.

RESULTS

Irrespective of whether the 15, 30, or 45 min criterion was employed to differentiate between short and long interbout intervals, the suckling index attained its maximal value during the month (4 weeks) immediately following parturition and generally declined during each successive month (4 week period) thereafter (Fig. 2). This was true for early and late mothers alike. The value of the index for the first month postpartum was near unity for the two groups of animals. In fact, so few protracted interbout intervals were realized during the first month that there was virtually no interindividual variation, a fact that precluded application of the *t*-test to the data. The value of the suckling index was consistently greater for the late mothers during every month subsequent to the first, again irrespective of what criterion was employed. The difference between the late and early mothers attained statistical significance for 2 months when the 15 min criterion was used, for 3 months when the 30-min criterion was employed, and for 5 months when the 45 min criterion was applied (Fig. 2). The earliest postpartum period for which significance was demonstrable was the second month when the 30 min criterion was used, and the third

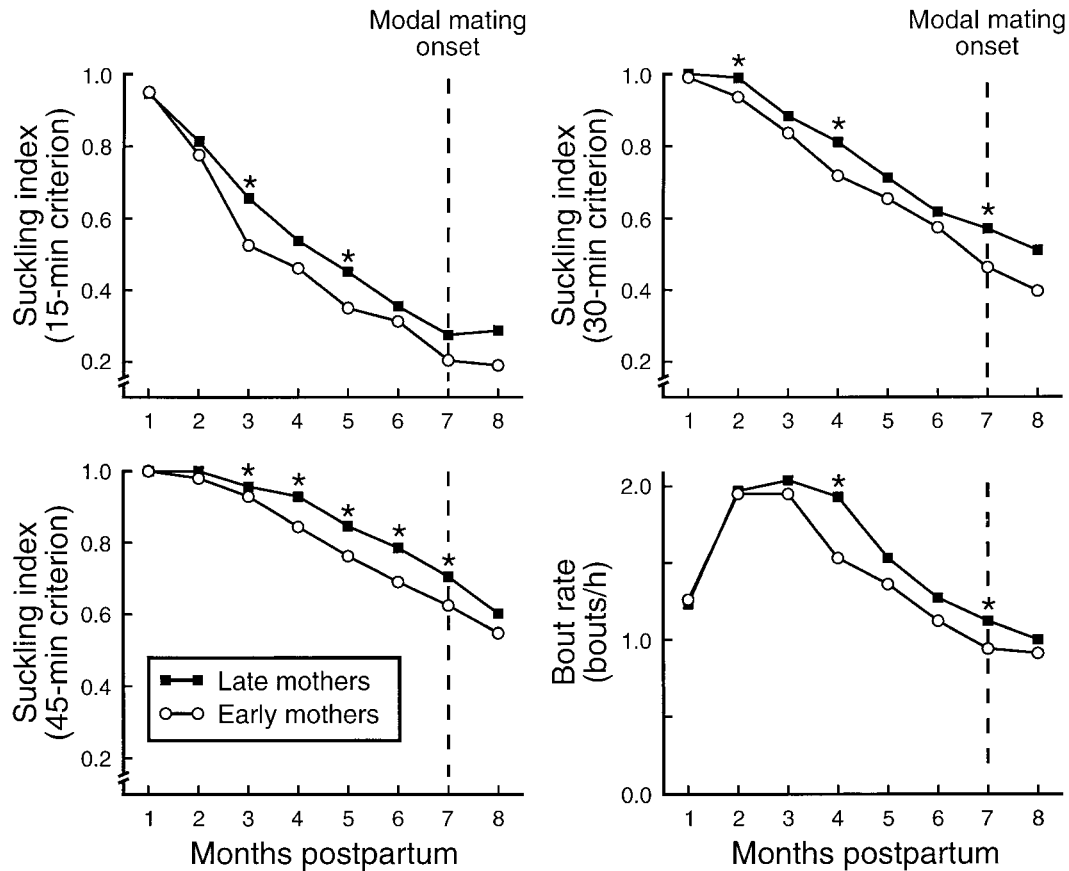


Fig. 2. Mean suckling index and bout rate scores for early and late mothers at Tughlaqabad during the first 8 months (32 weeks) postpartum. The modal mating onset month for all mothers is indicated. A month is defined here as a period of 4 weeks (see text). * $P < 0.05$ for monthly difference between early and late mothers.

month when either of the other two criteria was applied.

For most of our adult female subjects, early and late alike, the divergence of the suckling index curves preceded the onset of mating by many weeks. The modal onset week was the twenty-sixth; the earliest and latest were the nineteenth and twenty-ninth, respectively. With a month defined as 4 weeks long, the modal onset month was the seventh (Fig. 2); twelve of the 20 females (five early and seven late) resumed sexual activity at this time. Only two females (one late and one early) began mating as early as the fifth month, while another two (both late) began as late as the eighth month. Thus, the intensity with which mothers were suck-

led during the second and third month postpartum was not only predictive of how intensely they would be suckled during the following months but also of the rapidity with which they would regain their mating readiness.

The bout rate attained its maximal value later than did the suckling index, as late as the third month postpartum for the late mothers and their infants (Fig. 2). For early and late mothers alike, the bout rate increased sharply between the first and second months, and did not decline until the fourth 4 week period. The bout rates for the early and late mothers were not wholly congruent, however; from the third month of infant life onward, the mean rate of nipple

contact bouts was conspicuously higher for the late mothers, attaining statistical significance during the fourth and seventh months of infant life.

DISCUSSION

The progressive decline exhibited by each of the suckling index curves of Figure 2 is due to the fact that short interbout intervals (however they may be defined) constitute the great majority of the intervals realized by rhesus mother-infant pairs during the first 4 weeks postpartum but comprise a progressively smaller proportion during subsequent months. Recently, Johnson et al. (1993) presented a theoretical model of the lactational and environmental control of mating onset in female rhesus. One key tenet of the model is that interindividual differences in the intensity with which mothers nurse their infants (or infants suckle their mothers) manifest themselves very early postpartum, well before the mothers' resumption of sexual activity, and result in between-mother differences in the seasonal return of mating readiness. This tenet is here substantiated by the suckling index curves of Figure 2 (for analyses that strongly suggest the same is true for savanna baboons, *Papio cynocephalus* also see Altmann et al., 1978; Nicolson, 1987).

An uncritical inspection of the bout rate curve of Figure 2 would lead one to conclude that suckling intensity among rhesus does not peak until several weeks after birth, perhaps as late as the third month of infant life. This seemingly contradictory picture of the development of suckling stems from changes in the patterning of nipple contacts that are not indicative of changes in the intensity of nipple stimulation. In rhesus, interruptions of nipple contact (interbout intervals) are relatively few and markedly brief during the first 4 weeks postpartum. Therefore, suckling bouts are necessarily also few but extremely protracted. During the next 4 weeks, interruptions of nipple contact are more numerous, and, therefore, so are nipple contact bouts. Thus, the bout rate increases from the first to the second month postpartum precisely because the continuity of nipple stimulation (i.e., suckling intensity) declines. The inadequacy of

the bout rate as an index of the early development of suckling intensity is further indicated by the fact that this measure remains elevated during the third month of infant life even though relatively lengthy interruptions of nipple contact are beginning to be achieved at this time (see the 45 min index curve of Fig. 1).

It should be noted that the developmental changes in suckling intensity depicted in Figure 1 (e.g., the elevated bout rates during postpartum months 2 and 3) are not indicative of short-term developmental changes in the rate of neonatal growth or the production of milk on the part of rhesus mothers. Although a macaque infant's access to its mother's nipples declines precipitously during its first few months of life, the rate of weight gain (grams per day) by rhesus monkey infants is relatively stable during at least their first 6 months of life (Johnson and Kapsalis, 1995) and perhaps even their entire first year (Smith and Small, 1982). Furthermore, among provisioned Japanese macaques, the rate of milk transfer from mother to infant also remains relatively constant during the first 5–6 months postpartum (Tanaka, 1992), apparently because the total time spent engaged in nutritive suckling is conserved.

There are innumerable ways that suckling behavior can be described mathematically. For investigations of lactational infertility, the ideal index of suckling intensity would be one that mathematically is most sensitive to the parameters of nursing that mothers themselves are most sensitive to physiologically. Such an index would provide the greatest resolution for significance testing—that is, enable one to demonstrate statistically the occurrence of reproductively meaningful interindividual differences in suckling behavior even when such differences are small. Doubtless, if it was fully understood how the suckling stimulus disrupts the hypothalamic release of gonadotropin releasing hormone, we would have a clearer idea which parameters of nursing are physiologically most salient. However, as long as the physiology of suckling's contraceptive action remains incompletely understood, we take the position that the value of

a nursing index can be judged on the basis of the statistical resolution it affords.

When we employed a 45 min criterion to differentiate between long and short interbout intervals, the suckling index enabled us to demonstrate that the nursing behavior of early and late mothers at Tughlaqabad differed significantly throughout the third to seventh months postpartum. Fewer significant monthly differences were found when we employed a shorter criterion or when we examined suckling intensity by means of the bout rate. On this basis, we conclude that in rhesus the suckling index is a better measure of nursing intensity than is the bout rate not only because of the index's suitability for quantifying the early development of suckling (see above) but also because it is of greater physiological relevance, especially when a 45 min criterion is used in its computation. Our data indicate that the resumption of mating readiness is especially advanced in rhesus mothers when the interbout intervals they and their infants realize include a relatively large proportion of intervals of at least 45 min duration, perhaps because the effects of such interruptions of nipple contact are cumulative.

We are cognizant of the fact that had we defined suckling bouts differently the bout rate might have proven better at differentiating between the nursing behavior of our early and late female subjects. Certainly our definitions for the suckling bout and interbout interval are less stringent than those used in previous research on nonhuman primates (e.g., Lee, 1987; Stewart, 1988; Gomendio, 1989; Berman et al., 1993). In her study of captive rhesus, Gomendio (1989) considered suckling bouts to have commenced when any nipple contact, no matter how brief, was initiated and to be terminated when nipple contact had been interrupted by as little as 60 s of noncontact (the latter criterion having been adopted following a log survivorship analysis of interval lengths). To test whether intense suckling precludes conception, Gomendio (1989) compared the bout rates experienced by nursing mothers that conceived with those that did not, beginning with the fifth month postpartum. She found that, from the fifth to the ninth month, the rate at which nonconceiv-

ers nursed their infants was significantly greater than that of conceivers during just one 15 day period (the first half of the fifth postpartum month). Furthermore, from the sixth to the eighth month the bout rates of conceivers and nonconceivers were indistinguishable (see her Fig. 3). Thus, the data available do not suggest that adopting a more exacting definition of the suckling bout (i.e., one that places greater weight on brief, temporally isolated strings of nipple contact) would substantively improve the bout rate as an index of suckling intensity. Indeed, the results of Gomendio's (1989) study suggest that the reverse is true.

The problem of definition is not limited to research on nonhuman primate mothers. Between-study differences in the definition of the suckling bout have contributed to the "extreme" difficulty (McNeilly, 1993, p. 62; see also Labbok and Krasovec, 1990) investigators have had in identifying a pattern of suckling that, if maintained, will universally preclude the resumption of ovulatory cycling in women. Given the results of the present study, we wonder whether progress in this area might be advanced if, in addition to the conventional parameters of suckling used over the past 2 decades to quantify nursing, researchers also examined the proportion of interbout intervals exceeding some minimum duration. A first step toward assessing the value of such a change of focus might be a reanalysis of previously published data on the relationship between the patterning of breastfeeding and the postpartum onset of menses. Such a reanalysis would probably be more illuminating if the revisited data encompassed nighttime as well as daytime suckling. Although nocturnal nursing may not be critical for maintaining ovarian quiescence in macaque females (Gordon et al., 1995), the duration of lactational anovulation is prolonged significantly in women who breastfeed at night (Howie and McNeilly, 1982) and who therefore avoid exceptionally long interbout intervals.

Regardless of what utility the suckling index may have for human studies, it has two obvious advantages for research on nonhuman primate mothers. First, it is easily computed and, unlike the average interbout interval, can be meaningfully calculated even

when one does not know the full length of all intervals observed. Thus, the index is well suited for application to somewhat "messy" field data—that is, data like ours that include interbout intervals that were not observed in their entirety. Second, because its focus is the interval between nursing bouts rather than the suckling bout itself, the index is an appropriate means of making interspecific comparisons of the development of infant suckling. For example, the index would quantitatively demonstrate that rhesus females are suckled more intensely during the first few weeks postpartum (when their infants can suckle almost at will) than are mothers of same-aged infants belonging to species (e.g., *Presbytis* spp.) characterized by extensive allomothering (or kidnapping). The same could not be said of the bout rate since lengthy forced separations of mother and infant could potentially increase a mother's nursing bout rate even though the continuity of her nipple stimulation would be reduced.

The suckling index does have one obvious and important disadvantage relative to the bout rate, namely the need of lengthy focal sessions to document protracted interbout intervals (a disadvantage not shared by studies of lactational amenorrhea in women utilizing diaries rather than direct observation to collect data on the timing of breastfeedings). The data needed to calculate the bout rate can be collected during quite short focal sessions (e.g., 15 min), especially if one adopts a stringent definition of the nursing bout (see Berman et al., 1993). We believe that an as yet undescribed index of nursing intensity may possess advantages over both the bout rate and the suckling index, not necessarily just for rhesus females but perhaps for lactating women as well. Little research attention has been paid toward devising novel indexes of nursing that are mathematically more in tune with maternal physiology. We hope that the present paper will serve to stimulate investigation into this area.

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